

## Preferential consolidation of emotionally salient information during a nap is preserved in middle age

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### ABSTRACT

Sleep preferentially preserves aspects of memory that are most salient and valuable to remember at the expense of memory for less relevant details. Daytime naps and nocturnal sleep enhance this emotional memory trade-off effect, with memory for emotional components correlated with slow-wave sleep during the day and rapid eye movement sleep overnight. However, these studies have primarily sampled from young adult populations. Sleep and memory are altered by middle age, and the aim of the present study was to examine how age affects sleep-based mechanisms of emotional memory prioritization, using a daytime nap protocol to compare young to middle-aged adults. In both age groups, a nap soon after encoding scenes that contained a negative or neutral object on a neutral background led to superior retention of emotional object memory at the expense of memory for the related backgrounds. Sleep spindle activity during slow-wave sleep was related to memory for this emotionally salient information across the age range.

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### 1. Introduction

Our memories are not exact replicas of our experiences. Rather, both intrinsic and extrinsic properties of events determine what gets prioritized and promoted for a place in our memory. For example, salient information, especially if it is relevant for future use, is selectively consolidated, often at the expense of memory for less important information (Stickgold and Walker, 2013). This type of memory trade-off is observed when examining memory for complex emotional episodes, where memory for the emotionally salient focus of the episode is preferentially preserved, whereas memory for neutral, contextual detail is forgotten or suppressed (Kensinger et al., 2007). Importantly, the magnitude of the emotional memory trade-off increases over a period of sleep (Payne and Kensinger, 2011; Payne et al., 2008a), demonstrating that this phenomenon is not simply the product of attentional factors during encoding, but to active processes unfolding during sleep (Bennion et al., 2015).

Although several studies have substantiated this role for sleep in the selective consolidation of salient information, this research has primarily been conducted in young adults (Payne et al., 2008a, 2012). This limits our understanding of both the scope of the effect and the underlying sleep-based mechanisms. Both sleep

quality and episodic memory naturally begin to decline as we approach middle age (e.g., Ohayon et al., 2004; Verhaeghen and Salthouse, 1997). Moreover, the habits we form in middle age, including cognitive and sleep habits, may set the stage for healthy or unhealthy mental, cognitive, and physical health as we age. As such, a major goal of the present study was to investigate emotional memory and sleep in this understudied age group. To more fully understand the gap in knowledge this present study aims to address, we first need to review what is known regarding how memory and sleep are altered with age.

The ability to encode, consolidate, and retrieve new episodic experiences declines across the life span (Rajah et al., 2015), although most evidence comes from much older adults, and very little is known specifically about middle age. Among other brain areas, structural atrophy and functional changes have been revealed in regions heavily implicated in processing episodic memories (Aizawa et al., 2009; Buckner, 2004; Raz et al., 1997), notably the medial temporal lobe, specifically the hippocampus, and the prefrontal cortex (PFC). These changes begin to happen during the middle years of life (Raz et al., 2010). The profound reduction of cell density, synapses, and overall decreased plasticity in these areas impairs the ability to store new episodic information (Burke and Barnes, 2006). Beyond these structures individually, connectivity between the hippocampus and neocortex, vital for episodic memory consolidation and long-term retention, diminishes with age (Duverne et al., 2009; Grady et al., 2003; Morcom et al., 2003).

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However, there is conflicting evidence regarding memory impairments with age as they relate to emotional memory. Emotionally salient information consists of intrinsic characteristics that evoke an emotional reaction and lead to a perception of the valence of the stimuli (e.g., negative, neutral, or positive) and a level of associated physiological arousal (e.g., calming, exciting, agitating). Many studies have demonstrated that emotion processing is maintained with age (Kensinger, 2008; Mather, 2006) and that emotional information continues to be preferentially preserved over neutral information (Kensinger et al., 2002; Waring and Kensinger, 2009). Much of the influence behind why emotional information is remembered better than neutral information involves differences in attentional focus during encoding, with more attentional resources dedicated toward the emotional input (Hamann, 2001). Although such factors trigger an emotional trade-off in memory (Kensinger et al., 2004, 2007), factors including poststimulus elaboration (Steinmetz and Kensinger, 2013) and consolidation processes (Payne and Kensinger, 2010) modulate this initial effect. Evidence points to the idea that as we age, the emotional memory trade-off becomes more pervasive, perhaps due to the reduced ability to shift attention (Hasher, 2007), or a greater focus on the emotional center of the stimuli (Mather and Carstensen, 2003). While it appears that this type of nuanced selective memory for emotionally salient information persists with age, what is unknown is the role of sleep in the emotional memory trade-off effect as we age.

Along with changes in neural plasticity and circuitry described previously come alterations to sleep quality and quantity, which begin to occur as early as middle age (Ohayon et al., 2004). On a macro level, sleep latency, or the time to fall asleep, increases with age, as does the amount of time and duration of awakenings after sleep onset, leading to more fragmented and fragile sleep (Pace-Schott and Spencer, 2013). Sleep, overall, is shorter in duration, composed of increased lighter sleep (stages 1 and 2 sleep) as well as shorter nonrapid eye movement (NREM)-rapid eye movement (REM) cycles. While there is a more subtle reduction in REM sleep (Van Cauter et al., 2000; Pace-Schott and Spencer, 2013), most notably reduced is the deeper NREM sleep, called slow-wave sleep (SWS).

At the micro level, the most notable alterations to the properties of sleep beginning in middle age involve cortical slow wave activity (SWA, comprising slow oscillations 0.5–1 Hz and delta activity 1–4 Hz) and sleep spindles, which are thalamically generated bursts of activity (11–15 Hz) present throughout NREM sleep. Spectral power of cortical SWA is reduced with age, most prominently over the PFC during the first cycle of nocturnal sleep. This is the time when homeostatic sleep pressure is highest, typically leading to maximal expression of SWA in younger adults (Mander et al., 2013). This reduction in prefrontal SWA indicates a possible impairment in homeostatic sleep regulation as age increases (Dijk et al., 2010). Properties of the slow waves are also reduced, with shorter amplitude and less density and frequency of the slow waves (Carrier et al., 2011; Massimini et al., 2004). Similarly, spectral power and frequency of sleep spindles are reduced beginning in middle age compared to young adults (De Gennaro and Ferrara, 2003; Mander et al., 2014). In addition, spindle density and amplitude decrease, with the greatest reductions over the frontal cortex (Martin et al., 2013; Nicolas et al., 2001). While we are still discovering the reasons underlying these oscillatory alterations, recent research points to structural changes in brain regions with age. Of particular interest, but not exclusively, reduced gray matter density and atrophy in the PFC is related to slow oscillation activity (Dubé et al., 2015; Varga et al., 2016). In addition, as sleep spindles have been found to be temporally correlated with hippocampally generated sharp-wave ripples, bursts of activity of around 200 Hz

(Siapas and Wilson, 1998; Sirota et al., 2003), atrophy of hippocampal cells as age increases leads to sleep spindle impairment (Mander et al., 2017).

In young adults, the general theory of systems consolidation holds that reactivation of the neural networks associated with a learning experience leads to the strengthening of synaptic connections and a gradual redistribution of the memory into long-term cortical storage (see Diekelmann and Born, 2010; Payne et al., 2008b for review). It is thought that this reactivation optimally occurs during sleep, specifically SWS for declarative memories. Hippocampal sharp wave ripples, thought to induce long-term potentiation in the neural circuitry, and thalamically generated sleep spindles are temporally grouped by the upstates of the slow oscillations (Buzsáki, 1989, 1996; Pavlides and Winson, 1989). This is hypothesized to be the complex mechanism leading to the reinstatement of the neural network and consolidation of the memory during sleep. Slow wave activity is also theorized to downscale the synaptic potentials that increase with activity and deplete neural resources, functionally resetting the membrane potentials and increasing the plasticity of the cells (Tononi and Cirelli, 2003). At the same time, downscaling increases the signal-to-noise ratio, with highly potentiated networks representing learned experiences remaining above threshold and weaker traces falling below threshold, resulting in a memory trace that stands out after sleep.

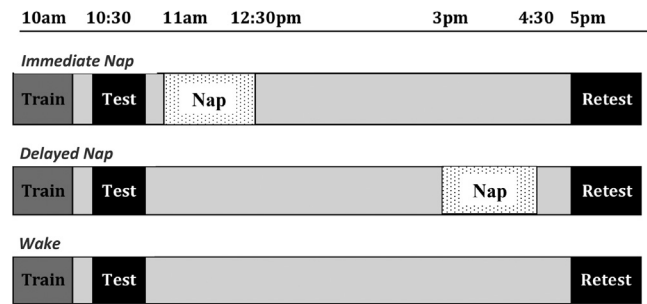
The question, then, is whether the functional relationship between sleep and memory consolidation remains the same as we age. As the macro and micro properties of these sleep mechanisms begin to be reduced with age, does this, in turn, lead to reduced memory in parallel? Do the same relationships that we see in young adults exist between sleep and memory as we age? Recent research supports this idea, with shorter, shallower, sleep related to impaired cognitive performance even with healthy aging (Backhaus et al., 2007; Cavuoto et al., 2016; Lo et al., 2016; Mander et al., 2014; Van Der Werf et al., 2009). Looking specifically at young and middle-aged adults, Backhaus et al. (2007) found evidence to support maintenance of the functional relationship between SWS and paired-associates memory, in that they saw both sleep and memory decline in middle age, leading to reduced sleep-dependent consolidation. Moreover, although memory was equal between age groups before sleep (specifically early night SWS-rich sleep), memory declined more for the middle-aged adults when retested after sleep. It may also be that the components of the complex sleep-based mechanism becomes uncoupled with age, such that slow oscillations and sleep spindles become uncoordinated, leading to memory impairments (Helfrich et al., 2017; Ladenbauer et al., 2017). However, it is possible that sleep and memory become functionally dissociated with age, with memory retention no longer predicted by sleep-based mechanisms, or not in the same manner, as in the young (Baran et al., 2016; Scullin, 2013). For example, Wilson et al. (2012) found no difference in sleep-dependent changes in memory for paired-associates between young, middle-aged, and older adults, although the sleep physiology likely differed between these age groups. Although they found preserved performance for all, they did not record sleep, so could not conclude anything of the relationship between sleep features and memory. It is possible that these studies are limited by the lens of their analyses, such as focusing more on the macro alterations in sleep with age (e.g., overall percentage of SWS) rather than examining the sleep and memory relationship at the micro level (e.g., spectral power of oscillations, topographical differences) (Mander et al., 2017).

The present study was undertaken with several carefully considered study design decisions in mind. First, although the emotional memory trade-off effect has been well examined in both young and elderly adults, it is not well understood in middle age.

We wanted first, to investigate emotional memory consolidation in this population, compared to well-studied young adults, and to then expand on the memory effect by exploring the impact of sleep on the selective consolidation of emotionally salient information. Second, as mentioned earlier, the work exploring the role of sleep in this selective consolidation has primarily sampled from young adults, typically undergraduates at universities and colleges. Using such “captive audience” samples is certainly convenient, and the reduced variability in such young, relatively healthy populations has provided a clear picture of the effect in this demography. However, there is a critical need to expand research to the greater population across a wider age range to examine the impact on aging in a generalizable way. Therefore, we chose to sample from the regional community rather than the student population to increase generalizability.

Third, although it has been well established that the magnitude of the emotional memory trade-off increases over a period of nocturnal sleep, primarily through the preferential preservation of the memory for emotionally foci of complex scenes (Payne and Kensinger, 2011; Payne et al., 2008a), only 1 study has examined this effect across a daytime nap (Payne et al., 2015). Similar increases in the emotional memory trade-off were observed during a nap compared with an overnight design. However, different properties of sleep were involved in selective memory for emotional components. REM sleep across a night, both total amount in minutes and percentage of total sleep time spent in REM sleep, was positively related to memory for negative objects (Payne et al., 2012). Emotional memories have been found to benefit from REM sleep, with theta activity (4–7 Hz) during REM sleep and high functional connectivity between the amygdala and the medial temporal lobe resulting in stronger memory traces for emotional information (Hu et al., 2006; Nishida et al., 2008; Wagner et al., 2001). While there has been a tendency to associate SWS and REM sleep with neutral declarative and emotional memory consolidation, respectively, this strict dichotomy seems increasingly unlikely as literature emerges implicating REM sleep in neutral (Groch et al., 2011) and SWS in emotional memory processing. Importantly, as related to the emotional trade-off effect, we recently found that properties of SWS (percentage and delta frequency power) during a daytime nap were positively related to negative object memory (Payne et al., 2015). This suggests a possible functional difference between nocturnal and daytime sleep in memory processing that needs to be further explored. The present study was designed to extend previous work (Payne et al., 2015) and provide further evidence and clarity of the contribution of daytime sleep physiology in the selective consolidation of emotional components of memory.

Finally, the present study design employed a novel between-subjects daytime nap design, with a nap either occurring immediately after encoding in the late morning or in the afternoon with a delay after encoding. The purpose of this design was 2-fold. We wanted to create 2 conditions that encoded and were tested at the same time of day that also had equal amounts of sleep and waking activity with the placement of the nap in time being the primary difference to address interference concerns that simply being “offline” during a nap passively protected the memory from external stimulation (see Fig. 1). We also wanted to manipulate the sleep stage composition of the naps, with the later nap consisting of proportionally more SWS based on the idea that homeostatic increases in sleep drive increases SWS during the subsequent sleep period. This design was previously implemented and concluded that a daytime nap with more SWS (i.e., the later nap compared with naps earlier in the day) promotes declarative memory consolidation (Alger et al., 2010). If properties of SWS (e.g., amount, power, spindle activity) during a nap underlie selective



**Fig. 1.** Protocol: all participants were trained and tested at the same time of day as one another, with encoding of the images at 10 AM, followed by baseline testing, and retest occurring at 5 PM. Nap groups had a 90-minute nap opportunity either at 11 AM (immediate nap condition) or 3 PM (delayed nap condition).

consolidation of emotionally salient information as previously reported (Payne et al., 2015), we anticipated we would see this more clearly using this dual-nap design.

In the present study, we aimed to compare the emotional memory trade-off effect in young (18–39 years) and middle-aged (40–64 years) adults using a dual-nap design. We hypothesized that a daytime nap would better preserve memory for the emotionally salient objects in encoded scenes at the expense of memory for the related neutral backgrounds, compared to remaining awake, thus increasing the magnitude of the negative memory trade-off. We predicted that, similar to our previous nap study in young adults (Payne et al., 2015), memory for the emotionally salient objects would be related exclusively to features of SWS (e.g., amount of SWS, spectral frequency markers, sleep spindles). Stemming from this prediction, we anticipated that if the later nap resulted in a higher proportion of SWS within the composition of the nap, this could result in superior retention of the salient information. Finally, although we expected to replicate the emotional memory trade-off effect in both young and middle age adults, whether we would see a similar relationship between properties of sleep and preferential memory preservation was more of an exploratory question, especially as so little is known about sleep and memory in middle age. Perhaps, we would see the relationship weakening with age, or perhaps different aspects of sleep would benefit memory as age increased. Notably, as we anticipated more stage 2 sleep in substitution for SWS with greater age, and spindle activity in NREM sleep is altered with age, perhaps this lighter stage of sleep is more involved in memory processing as we age.

## 2. Methods

### 2.1. Participants

Eighty participants (52 female) were recruited from the greater Northern Indiana community, through advertisements in local online publications (e.g., Craigslist), flyers around the University of Notre Dame campus targeting nonstudents, as well as through a preexisting pool of individuals who were concurrently participating in the longitudinal developmental Notre Dame Study of Health and Well-being. To increase external validity, this study aimed to minimize recruiting individuals currently enrolled at a 4-year university. Subjects recruited were aged 18–64 years (mean  $\pm$  SEM, 36.35  $\pm$  1.39 years) and in good health as assessed by an in-depth screening self-report, with no history of sleep disturbance, learning disorders, or mental/emotional problems. They were free from all medications known to impair or facilitate sleep, mood, and attention. Although we recruited evenly across this age range, we

intended to compare a young cohort to middle age adults. Consistent with the categorical boundaries set in the Notre Dame Study of Health and Well-being, we considered young adults as 18- to 39-year olds ( $n = 45$ , 32 female, mean age  $26.91 \pm 0.80$ ) and middle age adults as 40- to 64-year olds ( $n = 35$ , 20 female, mean age  $48.49 \pm 1.23$ ). All subjects received monetary compensation at the completion of their participation. This study was conducted according to the principles expressed in the University of Notre Dame Human Subjects Institutional Review Board, with all subjects providing written informed consent.

Prior to arrival to the laboratory, participants were contacted via email to ensure eligibility by administering the screening form. Participants were instructed to get no less than 6 hours of sleep the night before the experimental day and refrain from caffeine, alcohol, nicotine, and unnecessary medication 24 hours before and for the duration of the study. In accordance with these restrictions, they kept a 1-week sleep log to track their sleep/wake times, napping habits, and alcohol and caffeine intake prior to the experimental day. On arrival to the laboratory, participants were asked to sign a consent form explaining the nature of the research. Throughout the experimental day, they completed a demographics questionnaire as well as several other questionnaires to assess sleep habits and rule out psychopathology. These included the Pittsburgh Sleep Quality Index (PSQI; Buysse et al., 1989) to assess general sleep quality, the Morningness–Eveningness Questionnaire (MEQ; Horne and Ostberg, 1976) to assess morningness–eveningness tendencies, the Beck Anxiety Inventory (Beck et al., 1988), and State-Trait Anxiety Inventory (STAI, Spielberger, 2010) to assess level of state (STAI-X1) and trait (STAI-X2) anxiety, the Beck Depression Inventory–II (Beck et al., 1996) to assess depressive symptoms, the Positive and Negative Affect Schedule (PANAS; Watson et al., 1988) to assess positive and negative affect, and the Stanford Sleepiness Scale (SSS; Hoddes et al., 1973) to assess state sleepiness. These measures were used primarily to compare nap and wake groups to ensure they were similar to one another as well as to determine if any participant should be excluded because of scoring in elevated (i.e., clinical) ranges for depression or anxiety, which could impact both sleep and emotional memory formation.

## 2.2. Materials

### 2.2.1. Encoding materials

During the encoding task, participants viewed a set of 100 scenes that displayed either a neutral or negatively salient foreground object (50 of each valence) placed on a plausible neutral background (e.g., a deer or an angered grizzly bear in the forest, a taxi cab, or a taxi accident on a street). For each of the scenes, we created 4 different sets by placing 2 similar neutral objects (e.g., 2 images of a deer) and 2 similar negative objects (e.g., 2 images of angry bears) on 2 neutral backgrounds (e.g., 2 forests) to create 4 different but related scenes (Cunningham et al., 2014; Payne et al., 2008a, 2012, 2015). We used similar images to avoid the possibility that specific images may be more memorable, thus skewing the results. By varying the type of object (neutral or negative) and the background version (1 of the 2 paired backgrounds), 4 different lists of 68 scenes were created. Each participant saw only 1 list at encoding, which was randomly determined using a mixed Latin Square design.

### 2.2.2. Recognition materials

Memory for the images was tested during 2 sessions, baseline, which occurred immediately after encoding, and retest, which occurred later in the day. During both recognition tests, objects and backgrounds that had been viewed in the encoded complex scenes were presented separately (i.e., only the object or the background at

1 time) in random order. Each of these items had been previously studied was considered “old”. Intermixed with these “old” images were an equal number of objects and backgrounds, equated on measured ratings of valence and arousal, that had not previously been presented and were considered “new”. Half of the encoded information was tested at baseline and the other half at retest. Therefore, each recognition test consisted of 25 “old” negative objects, 25 “old” neutral objects, 25 “old” backgrounds previously paired with the negative objects, 25 “old” backgrounds previously paired with the neutral objects, 25 “new” images each of negative and neutral objects, and 50 “new” backgrounds, for a total of 200 images presented during each test.

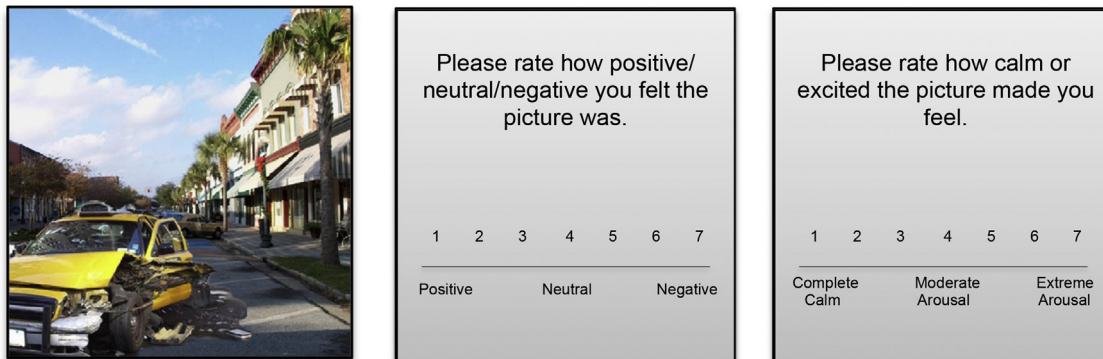
Most of the complex images used in this study have also been used in previous studies and have yielded normed ratings categorizing the scenes as either negative or neutral (Cunningham et al., 2014; Payne et al., 2008a; 2012, 2015). Because we altered a few of the images, we first conducted a pilot study ( $n = 24$ ) in part to evaluate the valence and arousal of the images to guide their placement into a negative or neutral category. In this pilot study, sampling from the undergraduate community of the university (aged 18–23 years), images were assessed using 7-point scales. All negative images had received arousal ratings of 5–7 (with higher scores associated with more arousing ratings) and valence ratings higher than 5 (with higher scores representing a more negative image). All neutral items (objects and backgrounds) had been rated as unarousing (arousal values lower than 3) and neutral (valence ratings between 3 and 5). Subjective ratings were also taken from participants in the present study for the full scenes at encoding, both to ensure the participants were attending to the stimuli, thus facilitating encoding, as well as to verify that the image ratings by this community population encompassing a wider age range were consistent with the undergraduate population ratings in the pilot study.

## 2.3. Procedure

At approximately 9:30 AM, participants arrived in the Sleep, Stress, and Memory Lab, signed informed consent, and completed a set of questionnaires (PSQI, MEQ, STAI-X2, Beck Anxiety Inventory, STAI-X1, and PANAS), which also included the SSS. They then incidentally encoded all 100 scenes with instructions to attend to the scene and make subsequent ratings of valence and arousal. Each scene was displayed for 3000 ms. After each scene was presented, participants were asked to make their self-paced ratings, first for valence and then level of arousal, on separate screens. Ratings were followed by a crosshair fixation point for 500 ms to direct attention and prepare for the next scene presentation. A self-paced baseline recognition test followed immediately after encoding, during which an image of an individual scene component (i.e., object or background) was presented centrally. Participants were required to press “0” if the image was considered “new” or “1” if they considered the image “old” (see Fig. 2). Participants were told at the end of the first session that they would be tested in this manner once more during the second session.

The present study was designed to have a wake control condition compared to 2 nap conditions in which participants obtained an equal amount of sleep and wake as one another, the primary difference being the positioning of the nap in time. Owing to scheduling constraints, participants were randomly assigned into wake control, immediate nap, or delayed nap groups in advance of their participation date. Wake and delayed nap participants were allowed to leave the laboratory following the baseline test with the instruction not to nap or consume caffeine, alcohol, nicotine, or unnecessary medication during the retention period. Those in the immediate nap group were prepared for polysomnography (PSG).

## Encoding Session

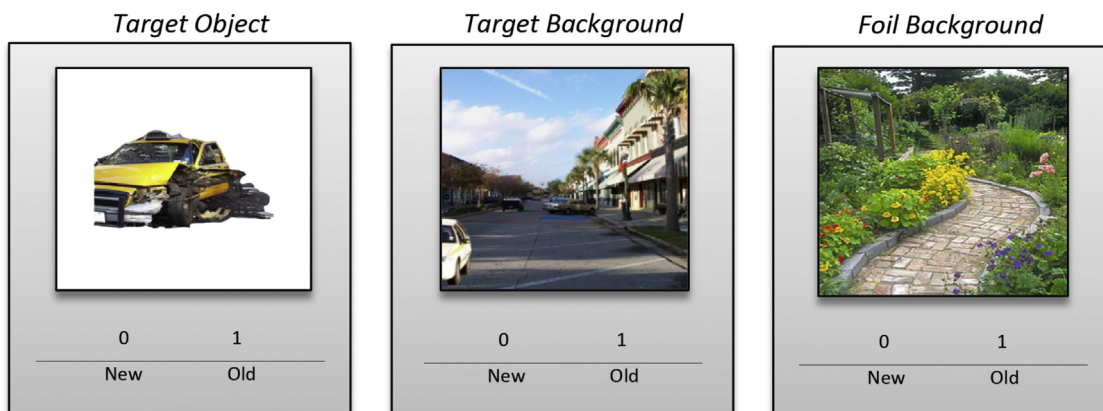


3000 ms

Self-paced

Self-paced

## Testing Sessions



*Target Object*

0 1  
New Old

*Target Background*

0 1  
New Old

*Foil Background*

0 1  
New Old

**Fig. 2.** Memory trade-off task: participants viewed complex scenes comprising either negative (i.e., taxi cab accident) or neutral foreground images placed on plausible neutral backgrounds. The images were presented for 3000 ms, followed by self-paced assessments of valence and arousal. Baseline testing occurred immediately after encoding, with half of the encoded objects and backgrounds, now presented individually and one at a time, intermixed with an equal amount of foils. Participants were required to decide if the images were ones they had not seen before (i.e., “new”) or ones they had seen before (i.e., “old”), using the keys 0 and 1, respectively, to indicate their choice. Retest occurred approximately 7 hours after encoding in the same manner.

At around 11 AM, immediate nap subjects were given a 90-minute PSG-recorded sleep opportunity lasting until about 12:30 PM. If participants obtained SWS or REM sleep during this time, they were allowed to sleep until they transitioned out of these stages to reduce sleep inertia and disorientation. After awakening, electrodes were removed, and these nap participants were allowed to leave the laboratory until the second session, approximately 4 hours later. Delayed nap participants returned to the laboratory at 2:30 PM and were prepared in the same manner for a 90-minute PSG-monitored nap opportunity, beginning at 3 PM. They were awakened at approximately 4:30 PM and allowed 30 minutes to recover for sleep inertia before beginning the retest session (see Fig. 1 for timeline).

All participants returned to the laboratory at 5 PM for the retest session and began by completing a second set of questionnaires similar to the previous session (Beck Depression Inventory, STAI-XI, PANAS, and SSS). Following these questionnaires, participants completed a psychomotor vigilance task (PVT, Dinges and Powell, 1985) to obtain objective measures of alertness and address the possible confound of an overall vigilance difference impacting task performance, rather than specifically sleep or lack of sleep accounting for performance differences. This cognitive test is a sustained reaction-time task that measures the average speed of a participants' response to a visual stimulus and demonstrates high

test-retest reliability (median intraclass correlation coefficients/ICC >0.8) and sensitivity (Basner and Dinges, 2012; Dorrian et al., 2005) to the effects of sleep deprivation (sensitivity = 93.7%), suggesting high convergent validity as well. After completing the PVT, participants were again tested via recognition on their memory for the remaining half of encoded material using the same method described previously (see Fig. 1 for protocol).

### 2.4. PSG recordings

Nap participants were monitored online using digital electroencephalography (EEG) acquisition software (Comet System-Grass/Twin PSG Clinical Software) using a standard polysomnographic montage, which included EEG(F3, F4, C3, C4, Cz), electrooculography, and chin electromyography channels, each referenced to contralateral mastoids. Each 30-s epoch of recorded sleep was scored blind to participants' behavioral task performance according to the standards of Rechtschaffen and Kales (1968). The PSG recording was scored visually as NREM stages 1, 2, SWS, and REM sleep, or wakefulness. EEG data were then filtered at 0.3–35 Hz (with a 60 Hz notch filter), and artifacts were visually identified and removed using the EEGLAB 13.4 (Delorme and Makeig, 2004) toolbox for MATLAB 9.1 (The MathWorks Inc, Natick, MA, 2012). Spectral analysis was then applied

to all artifact-free epochs of NREM and REM sleep during the nap. Fast Fourier transforms were carried out in MATLAB 9.1 to calculate mean absolute power spectral density ( $\mu\text{V}^2/\text{Hz}$ ) in the slow oscillation (0.5–1 Hz), delta (1–4 Hz), theta (4–7 Hz), and sigma (11–15 Hz) frequency bands to examine the frequencies associated with NREM SWS, sleep spindles, and REM sleep. Sleep spindle counts were obtained by filtering all artifact-free epochs of stage 2 sleep and SWS at 11–15 Hz and then applying the established automatic detection algorithm of [Ferrarelli et al. \(2007\)](#) using MATLAB 9.1. Total number of spindles, spindle density (spindles/total analyzed time in stage 2 and SWS), duration, amplitude, and power of the spindle events were calculated for frontal and central scalp electrodes (F3, F4, C3, C4) as well as the average across electrodes. The spindle range of 11–15 Hz was chosen based on prior research using this definition ([Lewis and Durrant, 2011](#); [Schabus et al., 2007](#); [Tamminen et al., 2010](#)).

### 2.5. Data analyses

We compared behavioral performance primarily within each age cohort to examine the impact of napping on memory in young (wake condition  $n = 15$ , immediate nap  $n = 15$ , delayed nap  $n = 15$ ) and middle age (wake  $n = 11$ , immediate nap = 12, delayed nap  $n = 12$ ) adults. For both baseline and retest sessions, memory for the objects and backgrounds was calculated separately for each valence (negative and neutral) as the number of items accurately remembered (i.e., hits) divided by the number of items originally viewed. To correct for response bias, we calculated corrected memory by subtracting the proportion of false alarms (“old” judgments to new pictures) of each object and background type from the proportion of hits ([Snodgrass and Corwin, 1988](#)) to obtain the measures we will refer to below as memory for each component (e.g., negative object memory, neutral object memory, and so forth). As a measure of the trade-off in memory, we further calculated the trade-off scores for each valence at each test by subtracting the memory for the associated backgrounds from the memory of the objects (e.g., corrected memory for negative objects minus corrected memory for backgrounds on which negative items were presented). These trade-off scores give us the magnitude of the difference between object and background memory. Performance changes over the retention period were the primary analyses conducted using repeated measured mixed analysis of variance (ANOVA). Correlations were conducted between sleep variables and behavior to investigate the nature of the role of sleep in performance benefits.

## 3. Results

### 3.1. Questionnaires and sleepiness measures

All analyses to compare questionnaire data were conducted between the 6 groups encompassing both experimental conditions (i.e., wake, immediate nap, delayed nap) and age groups (i.e., young and middle age). A 1-way ANOVA was conducted to verify that there were no differences between conditions or age groups on any questionnaire responses or sleep log data, such as amount of sleep achieved the night before the experimental day. There were no significant differences between groups on any measure of anxiety, depression, positive or negative affect, sleep quality, or morningness/eveningness tendencies. On average, all groups scored similarly as neither morning nor evening type on the MEQ, with only 3 individuals in separate groups scoring as an extreme morning ( $n = 2$ ) or extreme evening ( $n = 1$ ) chronotype. Excluding these extreme types from the analyses below did not change any of our findings. As for sleep and wake activity before arriving for participation, all subjects were compliant in getting more than

6 hours of sleep the prior night, with group averages ranging from  $7.42 \pm 0.19$  to  $7.78 \pm 0.30$  hours ( $p = 0.63$ ). All groups of subjects awoke, on average, between 6:45 and 7:45 AM the morning of the experiment, with no significant differences between groups. We found no difference in average number of daytime naps taken over the week before participation, either between age cohorts or between experimental conditions. With regard to sleep quality over the previous 1-month time interval, PSQI scores were not significantly different between groups (all  $p > 0.78$ ).

To verify that there were no group differences in sleepiness that could explain performance variations, we compared scores on the SSS and found no difference between groups either at session 1 ( $F_{5,74} = 1.51$ ,  $p = 0.20$ ) or session 2 ( $F_{5,74} = 1.64$ ,  $p = 0.16$ ). In addition, PVT comparisons revealed no significant differences between groups at retest in basic vigilance and alertness ( $F_{5,74} = 0.83$ ,  $p = 0.53$ ).

As previously mentioned, we previously conducted a pilot study to assess these images in part to determine the average valence and arousal ratings to categorize them into negative and neutral categories for the present study. We also had subjects in the present study rate the complete scenes at encoding, both to promote deeper encoding as well as verify our categorization of images. In examining the average image ratings per image in both the young and middle age cohorts, we determined that the image ratings were, overall, shifted toward a more positive direction. Within each of the 4 different lists, we found that the average valence and arousal ratings resulted in 16 of the 50 neutral images being categorized as positive (valence ratings 1 to 3, mean 2.60). We also found that 9 scenes in each list that were originally categorized as negative were consistently rated as neutral, and 1 neutral scene per list was rated as negative, thus leading us to recategorize these images for subsequent analyses. This yielded 42 scenes rated as neutral (valence 3.89, arousal 2.24) and 42 scenes rated as negative (valence 5.74, arousal 5.23) per list. In light of the literature regarding the possibility of a positivity bias with age, in which memory become biased to better remember more positive information compared with young adults ([Mather and Carstensen, 2005](#)), we examined whether there were differences in these ratings between young and middle age cohorts. As this task has been previously used to compare young to elderly adults with no sign of a positivity bias ([Waring and Kensinger, 2009](#)), we were not anticipating a difference. Correspondingly, between the cohorts, we found that it was the same images that fell outside of the original categorization, resulting in the same recategorization within each age cohort. In general, there was a slight shift toward positive in the middle age group for average valence ratings for both neutral (3.87 compared to 3.91 in the young group,  $t_{78} = 0.28$ ,  $p = 0.78$ ) and negative (5.68 compared to 5.79 in the young group,  $t_{78} = 1.05$ ,  $p = 0.30$ ) scenes. This positivity shift was not great enough to result in the image categorizations differing between groups.

### 3.2. The impact of napping on memory

We first analyzed the impact of napping on the selective consolidation of emotional memory within each age cohort to determine if the previously reported effect of sleep increasing the magnitude of the emotional memory trade-off was present. For both the young and middle age cohorts, we conducted a 3 (condition: wake, immediate nap, delayed nap)  $\times$  2 (session: baseline, retest)  $\times$  2 (valence: negative, neutral)  $\times$  2 (component: object, baseline) mixed ANOVA with condition as a between-subject variable and session, valence, and component as within-subjects variables. In the young cohort, a main effect of session ( $F_{1,42} = 341.41$ ,  $p < 0.001$ ) indicated that memory, in general, declined between baseline and retest sessions (see [Table 1](#)). We also found a main effect of component ( $F_{1,42} =$

218.15,  $p < 0.001$ ) demonstrating superior memory for objects over backgrounds. A 2-way interaction was found between valence  $\times$  component ( $F_{1,42} = 243.58, p < 0.001$ ), demonstrating the emotional memory trade-off effect, with better memory for negative objects ( $0.87 \pm 0.01$ ) compared to neutral ( $0.69 \pm 0.02$ ), but at the expense of memory for backgrounds paired with negative objects ( $0.41 \pm 0.02$ ) compared to those paired with neutral objects ( $0.57 \pm 0.02$ ). A second 2-way interaction between session  $\times$  component ( $F_{1,42} = 27.48, p < 0.001$ ) indicated that memory for objects was better retained across sessions, and this was further qualified by a 3-way interaction between session  $\times$  component  $\times$  group ( $F_{2,42} = 4.12, p = 0.02, \eta_p^2 = 0.16$ ). Independent  $t$  tests revealed that the immediate nap group retained memory over time for the objects significantly better than the wake control group ( $t_{28} = -2.65, p = 0.01$ ), but not the delayed nap group ( $t_{28} = 1.65, p = 0.11$ ). A 3-way interaction was also found between session  $\times$  valence  $\times$  component ( $F_{1,42} = 4.76, p = 0.04, \eta_p^2 = 0.10$ ), demonstrating that negative object memory is better retained over time than neutral object memory while memory for backgrounds paired with negative objects decays more than neutral backgrounds, thus increasing the magnitude of the emotional memory trade-off over time. However, this effect was further qualified by a significant 4-way interaction ( $F_{2,42} = 3.75, p = 0.03, \eta_p^2 = 0.15$ ). Post hoc comparisons revealed that the immediate nap group had significantly higher retention of memory for negative objects compared to both the wake ( $t_{28} = -3.22, p = 0.003$ ) and delayed nap ( $t_{28} = 2.22, p = 0.03$ ) conditions, and significantly more decay in memory for backgrounds associated with negative objects compared to the wake condition ( $t_{28} = 2.14, p = 0.04$ ). In other words, immediate napping resulted in the greatest increase in the magnitude of the emotional memory trade-off in the young cohort.

In the middle age cohort, we found a similar pattern of results. Main effects of session ( $F_{1,32} = 189.16, p < 0.001$ ) and component ( $F_{1,32} = 282.36, p < 0.001$ ) demonstrated a general decline in memory over time and superior memory for objects. A 2-way interaction was found between valence  $\times$  component ( $F_{1,32} = 142.95, p < 0.001$ ), again demonstrated the emotional memory trade-off effect. A second 2-way

interaction between session  $\times$  component ( $F_{1,32} = 10.55, p = 0.003$ ) indicated that memory for objects was better retained across sessions. Similar to the young cohort, middle aged adults showed a significant 4-way interaction ( $F_{2,32} = 4.53, p = 0.02, \eta_p^2 = 0.22$ ), again indicating a greater increase in the magnitude of the emotional memory trade-off in the immediate nap group. Post hoc comparisons revealed that the immediate nap group had significantly higher retention of memory for negative objects compared to the wake condition ( $t_{21} = -2.04, p = 0.05$ ) and more decay in memory for backgrounds associated with negative objects—significantly so compared to the delayed nap condition ( $t_{21} = -2.40, p = 0.03$ ), and at a trend level compared to the wake condition ( $t_{21} = 1.92, p = 0.07$ ).

Fig. 3 depicts the above findings for young and middle age using the calculated change in the memory trade-off scores (i.e., the difference in memory for objects and memory for backgrounds) across the retention period. The similarity of the pattern of the effect between the age groups for the negative memory trade-off can be seen with more clarity using this measure rather than examining object and background memory separately, as previously reported. When comparing the increase in the magnitude of the trade-off scores over time using  $t$  tests, no differences were found between conditions for neutral information for either young (all  $p > 0.37$ ) or middle age (all  $p > 0.32$ ). However, focusing on the increase in the negative trade-off, we see that for both age groups, the immediate nap condition had a significantly greater increase in the difference between memory for negative objects and background than both the wake (young  $t_{28} = -3.14, p = 0.004$ ; middle age  $t_{21} = -2.54, p = 0.02$ ) and delayed nap (young  $t_{28} = 2.52, p = 0.02$ ; middle age  $t_{21} = 2.17, p = 0.04$ ) conditions (Fig. 3).

To get a clearer picture of the relationship between age and memory, we ran a correlation analysis between age (as a continuous variable across the entire age range of 18–64 years) and baseline performance for the negative information to determine how age affected the ability to encode new salient information. We found significant negative correlations between age and negative object and associated background memory ( $r = -0.40, p < 0.001$ ;

**Table 1**  
Behavioral performance

Condition	Baseline (B)		Retest (R)		Change (R-B)		Trade-off change (R-B)
	OB	BG	OB	BG	OB	BG	
Young adults							
Neutral performance							
Wake	0.75 $\pm$ 0.03	0.66 $\pm$ 0.04	0.56 $\pm$ 0.04	0.43 $\pm$ 0.04	-0.19 $\pm$ 0.03	-0.24 $\pm$ 0.02	0.05 $\pm$ 0.04
Immediate	0.79 $\pm$ 0.03	0.72 $\pm$ 0.03	0.65 $\pm$ 0.04	0.47 $\pm$ 0.04	-0.15 $\pm$ 0.03	-0.25 $\pm$ 0.04	0.10 $\pm$ 0.05
Delayed	0.78 $\pm$ 0.02	0.69 $\pm$ 0.04	0.61 $\pm$ 0.04	0.42 $\pm$ 0.05	-0.17 $\pm$ 0.03	-0.28 $\pm$ 0.04	0.10 $\pm$ 0.05
Negative performance							
Wake	0.95 $\pm$ 0.01	0.47 $\pm$ 0.05	<b>0.77 <math>\pm</math> 0.04<sup>b</sup></b>	0.27 $\pm$ 0.03	<b>-0.18 <math>\pm</math> 0.03<sup>a</sup></b>	<b>-0.21 <math>\pm</math> 0.05<sup>b</sup></b>	<b>0.03 <math>\pm</math> 0.07<sup>c</sup></b>
Immediate	0.91 $\pm$ 0.02	0.59 $\pm$ 0.03	<b>0.87 <math>\pm</math> 0.02</b>	0.25 $\pm$ 0.04	<b>-0.04 <math>\pm</math> 0.03</b>	<b>-0.34 <math>\pm</math> 0.04</b>	<b>0.31 <math>\pm</math> 0.05</b>
Delayed	0.92 $\pm$ 0.02	0.58 $\pm$ 0.04	0.80 $\pm$ 0.03	0.31 $\pm$ 0.04	<b>-0.13 <math>\pm</math> 0.03<sup>b</sup></b>	-0.27 $\pm$ 0.04	<b>0.14 <math>\pm</math> 0.04<sup>b</sup></b>
Middle age adults							
Neutral performance							
Wake	0.72 $\pm$ 0.03	0.63 $\pm$ 0.04	0.51 $\pm$ 0.05	0.38 $\pm$ 0.05	-0.21 $\pm$ 0.03	-0.26 $\pm$ 0.05	0.05 $\pm$ 0.05
Immediate	0.77 $\pm$ 0.03	0.60 $\pm$ 0.06	0.58 $\pm$ 0.06	0.39 $\pm$ 0.06	-0.19 $\pm$ 0.05	-0.21 $\pm$ 0.05	0.02 $\pm$ 0.06
Delayed	0.73 $\pm$ 0.04	0.56 $\pm$ 0.05	0.62 $\pm$ 0.04	0.36 $\pm$ 0.06	-0.11 $\pm$ 0.02	-0.21 $\pm$ 0.05	0.10 $\pm$ 0.05
Negative performance							
Wake	0.87 $\pm$ 0.08	0.46 $\pm$ 0.06	<b>0.67 <math>\pm</math> 0.05<sup>b</sup></b>	0.24 $\pm$ 0.03	<b>-0.20 <math>\pm</math> 0.04<sup>b</sup></b>	<b>-0.21 <math>\pm</math> 0.05<sup>a</sup></b>	<b>0.01 <math>\pm</math> 0.08<sup>b</sup></b>
Immediate	0.88 $\pm$ 0.03	0.53 $\pm$ 0.07	<b>0.79 <math>\pm</math> 0.04</b>	0.16 $\pm$ 0.05	<b>-0.09 <math>\pm</math> 0.04</b>	<b>-0.37 <math>\pm</math> 0.06</b>	<b>0.28 <math>\pm</math> 0.07</b>
Delayed	0.84 $\pm$ 0.01	0.40 $\pm$ 0.05	0.75 $\pm$ 0.03	0.22 $\pm$ 0.05	-0.10 $\pm$ 0.02	<b>-0.18 <math>\pm</math> 0.04<sup>b</sup></b>	<b>0.09 <math>\pm</math> 0.06<sup>b</sup></b>

Mean  $\pm$  standard error of the mean.

All noted significant comparisons are between the immediate nap condition and either the wake or delayed nap condition, with notation adjacent to one of the latter conditions. Bolded values represent significant comparisons.

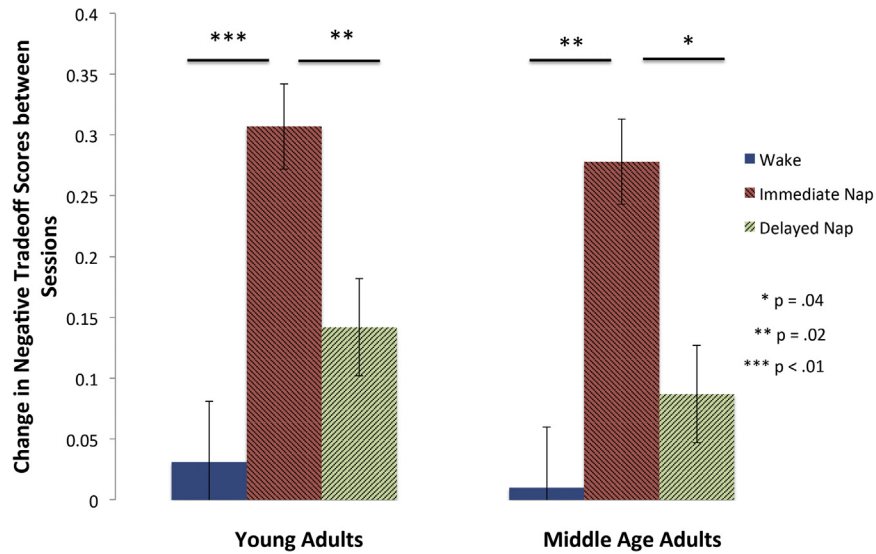
Trade-off change was calculated by subtracting the difference between object and background memory at baseline from the difference between object and background memory at retest.

Key: OB, object memory; BG, background memory.

<sup>a</sup>  $p < 0.10$ .

<sup>b</sup>  $p < 0.05$ .

<sup>c</sup>  $p < 0.005$ .



**Fig. 3.** Emotional memory trade-off effect across time by age cohort: the emotional memory trade-off score is the difference in negative object memory and related background memory, with a larger trade-off score representing a bigger difference in these memories. The figure above represents the increase in the magnitude of this trade-off score across the retention period for each condition for both the young adults (left) and middle-aged adults (right). The increase in emotional memory trade-off in the immediate nap condition was significantly greater than both the wake (young:  $t_{28} = -3.14, p = 0.004$ ; middle age:  $t_{21} = -2.54, p = 0.02$ ) and delayed nap (young:  $t_{28} = 2.52, p = 0.02$ ; middle age:  $t_{21} = 2.17, p = 0.04$ ) conditions.

$r = -0.27, p = 0.02$ , respectively) and background memory associated with neutral objects ( $r = -0.30, p = 0.01$ ), but not neutral object memory ( $r = -0.14, p = 0.20$ ), although also negatively correlated. However, when looking at consolidation of this information, measured by the change in performance across the 2 sessions, we did not see a significant correlation with any dependent variable of interest and age for any condition (wake group, all  $r < 0.22$ , all  $p > 0.28$ ; immediate nap, all  $r < 0.29$ , all  $p > 0.14$ ; and delayed nap, all  $r < 0.28$ , all  $p > 0.10$ ). These findings indicate that although encoding may be impaired with age in this task, the ability to consolidate the information does not appear to be.

### 3.3. Sleep stage parameters, EEG spectral power, and sleep spindles

As one of our predictions in using this dual-nap design was to examine the sleep stage composition between nap times, we first examined nap architecture in the immediate and delayed naps within each age cohort to determine if there was a shift in the relative amounts of stage 2, SWS, and REM sleep, as a function of increased sleep pressure throughout the waking day (Alger et al., 2010). Table 2 summarizes sleep parameters for both age cohorts for the 2 naps. The PSG recording for one subject in the young delayed nap condition contained a gap that prevented calculations

of the total sleep time or percentages of the specific stages relative to this time. Those data were thus excluded from subsequent sleep architecture comparisons and correlational analyses. Within the young cohort, we found no significant differences between immediate and delayed nap architecture (Table 2). Of particular interest, total sleep time (TST,  $t_{27} = -0.03, p = 0.98$ ) and the percentages of stage 2 ( $p = 0.54$ ), SWS ( $p = 0.66$ ), and REM sleep ( $p = 0.18$ ) were all similar between naps. In the middle age cohort, we likewise found no significant differences in naps (TST  $t_{22} = 0.82, p = 0.42$ ; stage 2  $p = 0.44$ ; SWS  $p = 0.78$ ; and REM sleep  $p = 0.65$ ). Therefore, we collapsed across the 2 nap times to compare young to middle age sleep quality based on prior research demonstrating altered sleep architecture with age. As detailed in Table 3, middle-aged adults had significantly shorter total sleep time (TST,  $t_{51} = 2.61, p = 0.01$ ), more wake after sleep onset (WASO,  $t_{52} = -3.55, p = 0.001$ ), poorer sleep efficiency ( $t_{51} = 2.94, p = 0.007$ ), more stage 1 ( $t_{51} = -3.93, p < 0.001$ ) and stage 2 sleep (trending,  $t_{51} = -1.87, p = 0.07$ ), and less SWS ( $t_{51} = 4.35, p < 0.001$ ) compared to young adults.

A limited number of comparisons were planned between sleep and both negative and neutral memory measures. Based on our a priori hypotheses and the previous literature regarding differing correlations with REM sleep and SWS and memory for salient

**Table 2**  
Sleep parameters for all conditions

Variables	Young adults			Middle age adults		
	Immediate nap	Delayed nap	p-value	Immediate nap	Delayed nap	p-value
TST	67.80 ± 3.56	68.00 ± 5.97	0.98	56.50 ± 6.34	47.88 ± 8.41	0.34
Onset latency	10.27 ± 1.78	8.89 ± 2.55	0.73	15.38 ± 4.59	9.42 ± 2.34	0.17
REM latency	50.05 ± 5.16	57.17 ± 7.86	0.41	59.33 ± 7.76	61.90 ± 4.37	0.82
WASO	15.10 ± 2.98	13.68 ± 3.80	0.80	24.42 ± 3.92	33.96 ± 5.86	0.13
Efficiency	72.89 ± 3.84	75.06 ± 6.47	0.80	58.33 ± 6.39	52.38 ± 8.87	0.53
Stage 1 %	17.13 ± 1.37	16.77 ± 3.38	0.95	28.48 ± 4.83	35.73 ± 5.58	0.21
Stage 2 %	41.39 ± 3.86	44.16 ± 4.94	0.65	53.58 ± 3.96	48.52 ± 5.07	0.45
SWS %	29.19 ± 4.33	32.13 ± 5.84	0.66	10.35 ± 3.94	8.49 ± 5.24	0.80
REM %	12.28 ± 3.28	6.94 ± 1.87	0.16	7.58 ± 3.14	5.76 ± 2.37	0.66

Mean ± standard error of the mean.

Key: REM, rapid eye movement; SWS, slow-wave sleep.

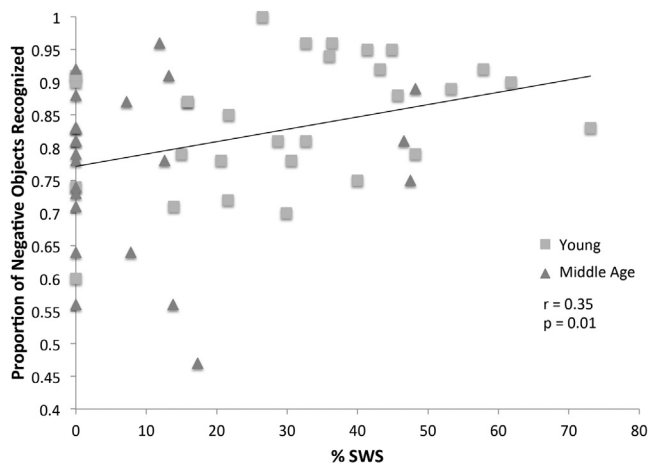


**Table 3**  
Comparison of young and middle age sleep

Variables	Young adults	Middle age adults	p-value
TST	67.90 ± 3.36	52.19 ± 5.23	<b>0.02</b>
Onset Latency	9.60 ± 1.51	12.40 ± 2.60	0.34
REM latency	53.42 ± 4.55	60.50 ± 4.48	0.31
WASO	14.41 ± 2.36	29.19 ± 3.59	<b>0.001</b>
Efficiency	73.94 ± 3.64	55.36 ± 5.38	<b>0.007</b>
Stage 1 %	16.96 ± 1.75	32.11 ± 3.69	<b>0.001</b>
Stage 2 %	42.73 ± 3.06	51.05 ± 3.19	0.07
SWS %	30.61 ± 3.54	9.42 ± 3.21	<b>&lt;0.001</b>
REM %	9.70 ± 1.96	6.67 ± 1.93	0.28

Mean ± SEM. Bolded values represent significant comparisons.  
Key: REM, rapid eye movement; SWS, slow-wave sleep.

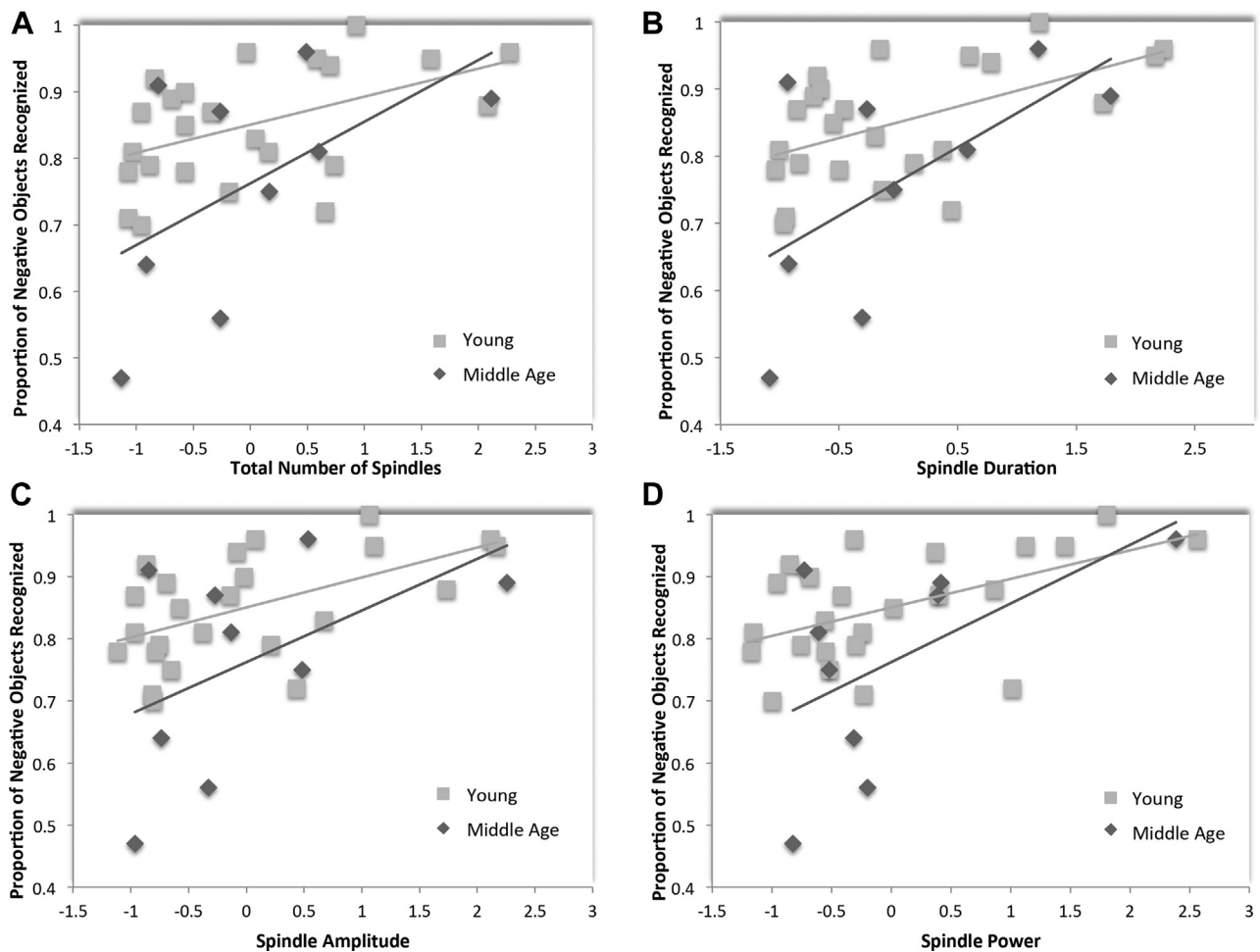
information, we focused our correlational sleep stage analyses on percentages of SWS and REM sleep. Because we were also interested in the impact of alterations to properties of stage 2 sleep (sleep spindle activity), we included this stage in separate, secondary analyses. Looking across all nappers, we found a significant positive correlation between the percentage of SWS and memory for the negative objects at retest ( $r_{53} = 0.35, p = 0.01$ , Fig. 4), which is similar to what was previously found using this emotional memory trade-off task and a daytime nap protocol (Payne et al., 2015). This supports our hypothesis that SWS during a nap facilitates the selective consolidation of emotionally salient information. Of the total number of subjects in the napping conditions, 25 young and 10 middle age adults obtained SWS. When we removed those who did not reach SWS from the analyses, the correlation remained significant ( $r_{35} = 0.34, p = 0.05$ ). No other significant correlations were found. When examining correlations between sleep stages and memory within each age cohort, we again saw a relationship between SWS and negative object memory in the young cohort both as a trend at retest ( $r_{29} = 0.36, p = 0.06$ ) and significantly assessing the change in performance across the retention period ( $r_{29} = 0.38, p = 0.04$ ), indicating better preservation of negative object memory with more SWS. No other correlations in either cohort reached significance but showed similar direction of the relationships as when looking at sleep across the age continuum.



**Fig. 4.** Correlation between SWS and negative object memory: the percentage of SWS was positively correlated with memory for the negative objects at retest ( $r_{53} = 0.35, p = 0.01$ ) across subjects (young = squares, middle age = triangles). This replicates the relationship we previously found in young adults (Payne et al., 2015). When we removed those who did not reach SWS from the analyses, the correlation remained significant ( $r_{35} = 0.34, p = 0.05$ ). SWS, slow-wave sleep.

To further clarify the role of sleep physiology in selective memory processing, we examined mean absolute spectral power ( $\mu\text{V}^2/\text{Hz}$ ), specifically looking at slow oscillations (0.5–1 Hz), delta (1–4 Hz), theta (4–7 Hz), and sigma activity (11–15 Hz). Comparing the age cohorts on spectral power, we found that middle age adults had significantly less slow oscillation and delta power ( $t_{32} = 2.85, p = 0.01$ ;  $t_{32} = 2.85, p = 0.01$ ) but similar power in the sigma and theta ranges (both  $p > 0.47$ ) as the young adults. Our correlational analyses revealed that the only significant relationships that emerged were from activity during SWS. We found that memory for negative objects at retest was significantly positively correlated with both slow oscillation power ( $r_{24} = 0.45, p = 0.03$ ) and delta power ( $r_{24} = 0.44, p = 0.03$ ) in the young adults. This complements the finding showing significantly higher slow oscillation and delta spectral power in the young versus middle age adults. To rule out the possibility that these correlations were driven by a single electrode site, we confirmed that slow oscillation activity was significantly, or nearly significantly, related to memory at all 4 electrode sites (C3  $p = 0.07$ , C4  $p = 0.04$ , F3  $p = 0.09$ , F4  $p = 0.01$ ). Similarly, delta power was related to negative object memory at all 4 electrodes as well (C3  $p = 0.04$ , C4  $p = 0.02$ , F3  $p = 0.09$ , F4  $p = 0.02$ ). These relationships between negative object memory and slow oscillations/delta power were not significant in the middle age group.

Analyses of sleep spindle activity during NREM sleep yielded significant associations that were complementary to our overall findings in that the only significant relationships to emerge were from SWS. Across all nappers, we found that memory for negative objects was positively related to all measured aspects of sleep spindle activity, but only during SWS, including the total number of sleep spindles ( $r_{33} = 0.46, p = 0.007$ ), spindle density ( $r_{33} = 0.45, p = 0.009$ ), average duration of spindles ( $r_{33} = 0.50, p = 0.003$ ), spindle amplitude ( $r_{33} = 0.50, p = 0.003$ ), and power of the spindle events ( $r_{33} = 0.52, p = 0.002$ ). As we examined the relationship between negative object memory and several different measures of spindle activity in one analysis, we corrected for multiple comparisons using the Bonferroni correction. All  $p$ -values surpassed the more conservative criteria of 0.01 to remain significant. To ensure that these associations were not the result of activity from 1 electrode, we verified that all electrode sites maintained the same significant positive relationship between negative object memory and all spindle variables, with the exception of sleep spindle density and the C3 and F4 sites, where only a trending relationship was seen ( $r_{31} = 0.30, p = 0.13$ ;  $r_{31} = 0.31, p = 0.09$ , respectively). When examining the associates within age cohorts, young adults showed significant positive relationships with the same variables (total spindle number,  $r_{24} = 0.47, p = 0.02$ ; density,  $r_{24} = 0.38, p = 0.07$ ; duration,  $r_{24} = 0.53, p = 0.008$ ; amplitude,  $r_{24} = 0.54, p = 0.006$ ; power,  $r_{24} = 0.52, p = 0.01$ ). Middle age adults also demonstrated similar relationships between spindle activity and emotional object memory but did not reach significance (all  $r$  values between 0.61 and 0.49,  $p$  values between 0.08 and 0.19, see Fig. 5). Using the Fisher  $r$ -to- $z$  transformation, we compared the difference between the young and middle-age correlation coefficients for memory and spindle feature associations and found no significant difference between any association (total spindles:  $z = -0.21, p = 0.83$ ; density:  $z = -0.67, p = 0.50$ ; duration:  $z = -0.21, p = 0.84$ ; amplitude:  $z = 0.16, p = 0.87$ ; power:  $z = -0.10, p = 0.92$ ). Comparing the young to middle age adults during SWS, the older group showed significantly fewer spindles ( $t_{31} = 2.17, p = 0.04$ ) that were smaller amplitude ( $t_{31} = 2.11, p = 0.04$ ) and nearly significantly briefer in duration ( $t_{31} = 1.96, p = 0.06$ ) spindles. However, spindle density and power were similar between the age cohorts (both  $p > 0.28$ ). Activity during SWS was our primary focus, but because we do observe a decrease in SWS while seeing an increase in stage 2 sleep with age, we also ran separate, secondary spindle



**Fig. 5.** Correlations between negative object memory and features of sleep spindles: negative object memory was positively correlated with features of sleep spindles for young and middle-age adults. Spindle measurements were transformed into z-scores within each age cohort to represent the associations on the same scale across cohorts. Strength of associations was similar between age cohorts. The associations were significant within the young adults. (A) Total number of spindles: young,  $r = 0.47$ ,  $p = 0.02$ ; middle age,  $r = 0.54$ ,  $p = 0.13$ , (B) spindle duration: young,  $r = 0.53$ ,  $p = 0.008$ ; middle age,  $r = 0.60$ ,  $p = 0.12$ , (C) spindle amplitude: young  $r = 0.54$ ,  $p = 0.006$ ; middle age,  $r = 0.49$ ,  $p = 0.19$ , (D) spindle power: young,  $r = 0.52$ ,  $p = 0.01$ ; middle age,  $r = 0.55$ ,  $p = 0.12$ .

analyses on stage 2 sleep. No significant correlations emerged from these analyses.

#### 4. Discussion

The present study aimed to investigate the impact of daytime napping on the selective preservation of salient information across an age range from young to middle age. Specifically, we examined both how the behavioral emotional memory trade-off effect manifested between young and middle aged individuals and whether sleep soon after encoding played an active role in preferentially preserving negatively salient memories while simultaneously suppressing or forgetting neutral contextual details. We observed that memory in the middle-aged adults was numerically poorer than young adults, with age negatively correlated with ability to encode. However, memory for emotional objects was still promoted above neutral information. Beyond this, we assessed the quality and quantity of sleep for all ages and found that sleep was significantly worse in many ways in the middle-aged adults. Our observations fit the literature describing the alterations that develop in sleep architecture with age, with shorter total sleep time and more frequent arousals during a period of sleep. Furthermore, we confirmed that a middle-aged population obtains significantly less SWS and more of stages 1 and 2 sleep, resulting in lighter and less consolidated sleep.

However, despite these general declines in sleep and memory, we still revealed that napping immediately after learning selectively preserved memory, particularly emotional memory, and led to a greater increase in the magnitude of the emotional memory trade-off over time.

We note that our experimental groups had different experiences and possibly different expectations throughout the experiment, as the wake condition did not experience electrode hookup and did not undergo an in-laboratory nap with PSG recording. Aside from the activities specific to the recording of the nap, however, laboratory experiences were similar between groups. As we found no differences between conditions for any questionnaire measure, PVT score, or baseline memory performance, we do not think that the different experiences between conditions played a role in the results we obtained.

There is a dearth of research that focuses on the middle age in general, but specifically when examining the relationship between sleep and memory consolidation. The few studies that have looked at this population have produced equivocal findings, with some studies reporting preserved (Wilson et al., 2012) or reduced (Backhaus et al., 2007) sleep-dependent performance changes in declarative memory. To our knowledge, the present study is the first to focus on the middle age population examining the kind of nuanced, selective memory seen using the trade-off task,

particularly in this highly novel napping paradigm. Although studies tend to compare the extremes of young versus elderly adults to draw out the differences brought about by alterations in memory and sleep with aging, few studies investigate those of the age where these alterations begin to occur, leaving a gap in knowledge regarding this population.

One unexpected finding that this study revealed was that when sampling from a wider age range from the greater community, not focusing on a narrow population of young undergraduate university students, we did not observe the expected increase in the amount of SWS participants obtained on average during the late nap. Process S, or the homeostatic sleep drive posits that there is an increase in sleep pressure and need for homeostatic regulation, indexed by the amount of SWS, with SWS increasing exponentially as a function of how much time is spent awake before sleep (Knowles et al., 1986). Previous research has supported that this increase in SWS occurs (Carskadon and Dement, 2005; Tononi and Cirelli, 2006) and that it may be related to differential memory processing (Alger et al., 2010). However, research regarding the relationship between the time-based shift in sleep architecture as a modulator of memory processing has sampled heavily from the young student population. Perhaps the unique sleeping habits and intensive learning experienced by a typical undergraduate results in a more pronounced increase in SWS over time, particularly as evidence supports increases in properties of slow wave activity after intensive learning (Eschenko et al., 2008; Huber et al., 2004; Tononi and Cirelli, 2003). Future studies will need to replicate the lack of this shift in sleep architecture we observed in the present study to delve into the possible reasons behind it.

However, being that our study found that the sleep composition was relatively equal between the immediate and delayed naps in our age cohorts, the story here is about the benefits of immediate napping compared to the consequences of delaying sleep. Between the 2 nap conditions, the total amount of time asleep, as well as the time spent awake and engaged in everyday activity was equal, with the placement of the nap in time being the primary difference. This design helps to address potential criticisms that any benefits in the nap group are due to passive interference, such that the nap group performs better simply because they were protected from external stimuli during the whole of the retention period. If this were the only factor, then both naps in the present study would equally passively protect the memory and would perform similarly to one another. However, other factors may play a role, such as the natural deterioration of memory due to interference prior to a delayed nap that may reduce what memory is available to consolidate. Moreover, there is the idea that a limited window of time during which sleep can facilitate consolidation of labile memory traces, after which sleep will not be as effective (Mednick et al., 2011). The design we used is reminiscent of another common sleep study design in which learning, sleeping, and testing occurs across a 24- (or 48-) hour period. In these studies, sleep either occurs immediately after learning in the evening (commonly called a sleep-first condition) or after a full day of wake filled with everyday waking interference following learning in the morning (called a wake-first condition), with testing occurring 24 hours after learning. Notably, these studies confirm that sleeping soon after learning leads to stabilization and protection of the memory from subsequent interference (Talamini et al., 2008; Van Der Werf et al., 2009), including preferential preservation of emotional information (Payne et al., 2012). The present study demonstrates that these immediate benefits can even be observed over shorter retention periods, suggesting that this type of immediate sleep can be used as a technique for optimal memory.

The differences between young and middle-age adults in regard to the spectral composition of sleep fall in line with what has previously been found, particularly regarding the reduction of slow oscillatory and delta power with age. In addition to these reductions, we did not see the same correlations between memory for the emotional components of the images and power in these frequency ranges during SWS in the middle-aged subjects, as we observed in the young subjects. These findings may indicate that delta and slow oscillatory activity are less important or less actively involved in the preferential consolidation of salient information as we age. This could lend support to the idea that there is a weakening of the functional relationship between sleep and memory with age (Scullin, 2013). Indeed, although we found that the percentage of SWS during the nap was positively correlated with negative object memory across all participants, this was clearly driven by the young adults, with far weaker relationships in the middle-aged adults. However, looking to the sleep physiology within SWS, we see similar relationships between memory for negative information and sleep spindle features. This suggests, perhaps, that looking beyond the stage of SWS as a whole and focusing on specific features of sleep within this stage can reveal ongoing active beneficial processes across age.

There are a few possible explanations for our results. It is clear by looking at the behavioral data that sleep, overall, plays a significant role in the preferential preservation of salient information at the expense of memory for background detail, as demonstrated by the same pattern of the effect between age cohorts, with immediate sleep-yielding superior memory. It may be that the underlying sleep-based mechanisms (i.e., collaboration between slow oscillations and sleep spindles actively leading to systems consolidation) are altered with age and that another, as of yet unknown, mechanism becomes more involved (e.g., sleep spindles alone). We may also be limited by how we are measuring sleep, relying on low-density EEG recordings, which may prevent us from uncovering the specifics of the change in mechanism. Using high-density EEG recordings in the future may allow us to tease out topographical differences in activity and uncover an altered mechanism. Extending this design over a wider age range that also encompasses older adults would also allow us to infer if the relationship between the known sleep-based mechanisms (i.e., SWS and spindles) and memory further changes with age. This is particularly important in light of new evidence that demonstrates the importance of the phase-coupling between slow oscillations and sleep spindles and how they may become uncoupled with age and/or cognitive impairment/Alzheimer's disease (Helfrich et al., 2017; Ladenbauer et al., 2017; Mander et al., 2017). There is great potential of developing an intervention strategy to boost sleep physiology and improve memory if the relationship persists with age. In young adults, interventions such as increasing SWA (Westerberg et al., 2015) or sleep spindles (Ladenbauer et al., 2016; Mednick et al., 2013) through stimulation or pharmacological manipulations have enhanced memory performance, although whether this would be as successful in healthy older individuals has yet to be examined.

We caution, however, that the correlations we detected between sleep and performance, while intriguing, should be taken with a grain of salt, as our nap design resulted in many participants on the older end of the age range not obtaining any SWS. Only 10 of the 24 middle age adults obtained SWS in their naps, and only 9 of those subjects had detectable spindle activity. Thus, our observation of a dissociated relationship between memory and SWS (i.e., weaker with percentage and delta/slow oscillation power yet similar spindle power) may stem from these correlational analyses being underpowered, in contrast to our behavioral analyses, which were appropriately powered. In other words, our ability to fully perceive

the functional relationship between sleep physiology and memory may have been impeded by the very nature of the aging brain in sleep, with reduced SWS, delta, slow oscillatory, and spindle activity reducing the number of participants included in the analyses.

Nevertheless, the present study adds support to the idea that daytime and nocturnal sleep contribute to the consolidation of salient information in functionally different ways, with SWS actively facilitating memory during daytime naps, most clearly in the younger participants. Similar to what we revealed in a previous study, memory for the emotionally salient focus on experiences was related to the relative amount of SWS and delta frequency power during this stage (Payne et al., 2015), with further evidence from the present study demonstrating a role for slow oscillatory power and sleep spindle activity during this stage as well. It is important to conclude from these sleep analyses that the *only* aspect of memory that was found to be related to sleep physiology was emotional object memory, not any form of neutral memory, reflecting preferential consolidation. These findings open the door to future studies designed to answer the question of why this differential contribution of SWS during the day and REM sleep overnight may occur. One thing to consider is that daytime naps have considerably less REM sleep than nocturnal sleep, given the way in which we cycle through sleep stages and the shorter duration of a nap. In the present study, 19 of 30 young adults and 11 of 24 middle-aged adults in the napping conditions obtained REM sleep. This is similar to, or more than in the case of the young adults, the number of subjects obtaining REM sleep in another nap study examining emotional memory consolidation. Nishida et al. (2008) found an association between REM sleep, and theta within REM sleep, and emotional memory consolidation. However, they did not examine selective consolidation, but rather consolidation of scenes as a whole. Our study not only brings further into question previously held ideas about REM sleep predominantly benefitting emotional memory but also replicates our previous SWS and selective consolidation of emotional components findings (Payne et al., 2015). In our previous study, 16 of 22 young adults obtained REM sleep. We speculate that perhaps circadian phase differences and factors such as neurohormonal cycles, such as the natural rise in cortisol that coincides with REM-rich nocturnal sleep, may be important in explaining the differential contribution of REM overnight and SWS during the day for selective emotional memory consolidation. It is important, although, in any future study, to dig down into the different levels of sleep, from gross sleep staging, to spectral composition, to phenomena occurring during sleep such as sleep spindles, to gain a clear picture of the mechanisms of selective consolidation and how they may change with age.

In summary, we demonstrated the importance of obtaining sleep soon after learning for superior selective consolidation of emotional memories, an effect that was robustly seen across young and, for the first time, middle-aged adults. While we found that properties of SWS, such as the relative amount, frequency markers (i.e., delta, slow oscillations) were involved in this preferential preservation of salient information, these relationships were primarily driven by the young adults. Although sleep spindle activity during SWS appeared to be associated with memory for negative information in both young and middle-age adults, this relationship did not reach significance for the middle-age adults, likely due to far fewer middle-age adults producing spindles. The present study serves as a first step to discover whether the functional relationship between memory, particularly memory for important, adaptive experiences, and known mechanisms of sleep physiology-based consolidation persists into the middle age and beyond. Uncovering this relationship is crucial, as it is possible for the future development of interventions to boost properties of SWS, possibly leading to the improvement of memory that normally declines as we age.

## Disclosure statement

The authors have no actual or potential conflicts of interest.

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